

## NOTES ON OTHER MARSUPIALS.

*Phascolarctos cinereus*. Embryo of G.L. 4 mm.

Our earliest stage of *Phascolarctos cinereus* measures 4 mm. at its greatest length. The outer wall of the optic vesicle is thickened and flattened and the optic stalk is in wide communication with the fore-brain.

Situated postero-medially to the optic vesicle on each side is a large premandibular head-cavity, the long axis of which lies in the sections in an obliquely antero-posterior direction. From the posterior and postero-lateral walls active proliferation is taking place by means of hollow buds which are growing out from the cavity, a solid mass of cells being formed by the thickened walls of one bud running into those of another. Next the fore-brain the walls consist of a single epithelial layer, which in some places, however, is not distinctly seen.

Unfortunately, this embryo is not well preserved and the abducens muscle-mass is very difficult to distinguish from the thickened posterior wall of the head-cavity.

## Embryo of G.L. 7.5 mm. (Text-fig. 20.)

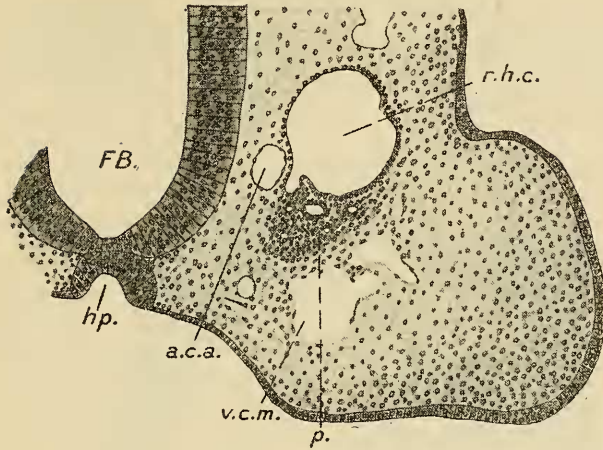
An older embryo, measuring 7.5 mm., shows the optic vesicle much further invaginated and the primordium of the lens in the form of a thickened hollow ingrowth from the ectoderm.

The head-cavity has increased considerably in size, having a maximum diameter of .30 mm.  $\times$  .26 mm. (text-fig. 20, *r.h.c.*), and its antero-ventral portion has grown forwards above the optic vesicle. The whole of the posterior wall is thickened; hollow buds, many of which are long and tubular, run out into a mass of closely packed cells, the entire region appearing as an irregular mass pitted with small hollow spaces (text-fig. 20, *p.*). The wall next the fore-brain, as in our first stage, is composed of a single layer of cells.

The abducens muscle-mass, which is clearly recognisable, consists of a narrow postero-dorsal portion lying along the medial side of the vena capitis medialis; this continues into the larger anterior part, which extends obliquely forwards and downwards postero-laterally to the head-cavity to meet the intermediate mass. The latter stretches forwards just above the optic vesicle into a bulbous extension, the primordium of the m. obliquus superior, and runs downwards into the maxillo-mandibular mesenchyme; it is also connected with the postero-lateral wall of the head-cavity.

The oculomotor nerve is well developed, its distal end terminating some distance from the head-cavity.

Text-figure 20.



*Phascolarctos cinereus*. G.L. 7.5 mm.

Horizontal section through the head (S 5-3 7), passing immediately above the optic vesicle and just below the middle of the right head-cavity (*r.h.c.*). The posterior wall of the cavity is actively proliferating (*p.*). Size of cavity 30 mm.  $\times$  26 mm.  $\times$  110 and reduced by  $\frac{1}{4}$ .

*a.c.a.* = arteria cerebri anterior. *FB.* = Fore-brain. *hp.* = hypophysis.

Embryo of G.L. 9 mm. (Text-fig. 21.)

At 9 mm. the optic vesicle is closed except on the medial side where the hollow optic stalk runs inwards to the fore-brain. The lens has now the form of a vesicle and is no longer connected with the ectoderm.

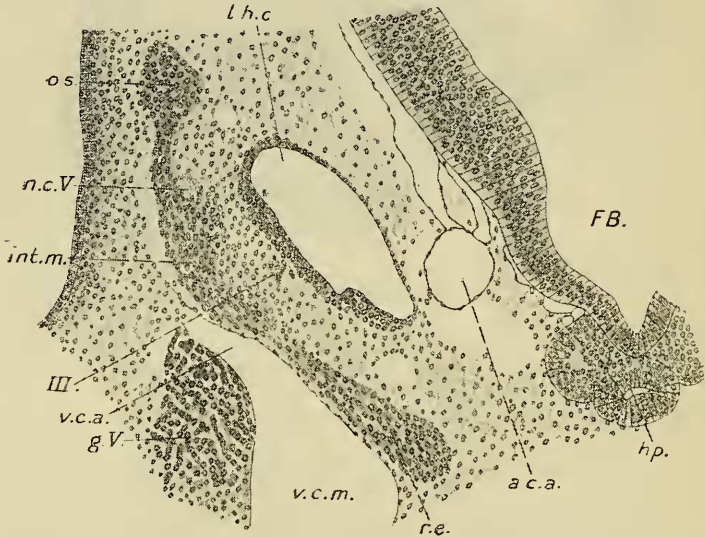
The head-cavity is still larger (text-fig. 21, *l.h.c.*) and resembles in shape that of *Trichosurus*, embryo (*a*) 7.25 mm. A large bud is present on the dorso-lateral side, the posterior and ventral walls of which are thickened, whilst the whole of the postero-lateral wall of the cavity is actively proliferating.

The primordium of the m. obliquus inferior runs out from the postero-lateral side of the cavity behind the optic vesicle, and medial to this muscle there is an indication of the future m. rectus inferior.

The abducens muscle complex is well marked in this embryo, and its connection with the intermediate mass and the m. obliquus superior is clearer than in any of the embryos of *Trichosurus* examined (text-fig. 21). The abducens nerve runs into the postero-dorsal portion which is situated in its usual position medial to the vena capitis medialis; the anterior portion (text-fig. 21, *r.e.*) lies along the postero-lateral side of the cavity in

front of the vena capitis medialis and stretches laterally into the intermediate mass (text-fig. 21, *int.m.*). The latter extends, on the one hand, forwards and upwards to be connected by a narrow band of cells with the *m. obliquus superior* (text-fig. 21, *o.s.*) and on the other, downwards and backwards to join the maxillo-mandibular mesenchyme.

Text-figure 21.

*Phascolarctos cinereus*. G.L. 9 mm.

Horizontal section through the head (S 4-2-6) passing through the left head-cavity (*l.h.c.*), about a quarter of the way down, and showing the *m. obliquus superior* (*o.s.*) growing forwards from the intermediate mass (*int.m.*), this being also united with the abducens muscle-mass (*r.e.*). In the next few sections further ventrally, the intermediate mass is joined with the postero-lateral wall of the head-cavity at approximately the region marked \*.  $\times 110$  and reduced by  $\frac{1}{2}$ .

*a.c.a.*=arteria cerebri anterior. *FB.*=fore-brain. *g.V.*=Gasserian ganglion. *hp.*=hypophysis. *n.c.V.*=naso-ciliary branch of the trigeminal nerve. *v.e.a.*=vena cerebri anterior. *v.c.m.*=vena capitis medialis. *III.*=oculomotor nerve.

The *m. obliquus superior* is a compact mass of cells lying antero-laterally to the cavity above the optic cup. The intermediate mass a few sections below the level of text-fig. 21 is attached to the extreme postero-lateral wall of the cavity.

The oculomotor nerve runs down close to the postero-lateral wall of the premandibular cavity (text-fig. 21, *III.*) and below the level of the same splits up into many fibres near the point of origin of the *m. obliquus inferior*.

## Embryo of G.L. 11 mm.

In our next embryo, which measures 11 mm., all traces of the head-cavity have disappeared, the m. obliquus inferior has begun to move forwards below the eye and the m. rectus inferior is further developed. *Phascolarctos* has now reached a stage in development intermediate between that of the *Trichosurus* embryos of 10 and 11 mm.

The later history of the eye muscles is similar to that of *Trichosurus* and need not again be described.

## PHASCOLOMYS MITCHELLI. (Text-fig. 22.)

The two youngest embryos of *Phascalomys mitchelli* measure at their greatest length 9 mm. and 8.5 mm. respectively; the former is slightly the younger of the two.

The optic vesicle is closed and the optic stalk is in wide communication with the fore-brain; the lens is a hollow vesicle shut off from the ectoderm.

Text-figure 22.

*Phascalomys mitchelli*. G.L. 8.5 mm.

Longitudinal section (S 2-1-1) passing through the lateral side of the right head-cavity (*r.h.c.*) and showing the proliferation from the dorso-lateral wall (*d.l.*) and the primordium of the m. obliquus inferior (*o.inf.*). The intermediate mass (*int.m.*) situated between the cavity and the Gasserian ganglion (*g.V.*) is seen to be connected with the maxillo-mandibular mesenchyme (*max.md.*) by a band of cells lying just on the medial side of the vena orbitalis inferior (*v.o.i.*).  $\times 110$  and reduced by  $\frac{1}{4}$ .

*a.c.a.*=arteria cerebri anterior. *op.c.*=optic cup. *v.c.a.*=vena cerebri anterior. *v.c.m.*=vena capitis medialis. *v.o.i.*=vena orbitalis inferior. III.=oculomotor nerve.

In the 9 mm. embryo the head-cavity is large and triangular in shape, resembling that of the 9 mm. stage of *Phascolarctos*, while in the 8.5 mm. specimen it is much reduced in size (text-fig. 22, *r.h.c.*). In both embryos a dorso-lateral proliferating muscle-bud is present (text-fig. 22, *d.l.*), and the m. obliquus inferior extends down from the ventro-lateral wall posterior and ventral to the optic cup (text-fig. 22, *o.inf.*).

The anterior portion of the abducens muscle complex is joined with the intermediate mass, and the connection of the latter with the maxillo-mandibular mesenchyme by means of a wide band of cells is well seen in the 8.5 mm. embryo (longitudinal series) (text-fig. 22).

The m. obliquus superior has the same appearance as in the 9 mm. stage of *Phascolarctos*; on its inner border it practically surrounds the supra-orbital branch of the trigeminal nerve.

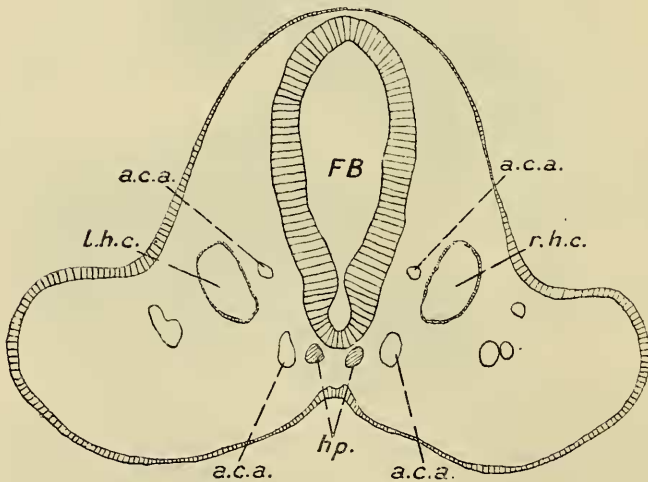
The oculomotor nerve is prolonged ventrally into the m. obliquus inferior and the abducens nerve runs into the hinder end of the postero-dorsal portion of the abducens muscle complex.

The examination of the two older stages, measuring 15.5 mm. and 17.5 mm. respectively, shows that the further development of the eye muscles proceeds as in *Trichosurus*.

#### MACROPUS RUFICOLLIS. (Text-figs. 23 & 24.)

Only one embryo of *Macropus ruficollis*, with a maximum length of 6.7 mm., came under observation. The optic vesicle is

Text-figure 23.



*Macropus ruficollis*. G.L. 6.7 mm.

Horizontal section through the head (S 4-2-1) showing the head-cavity on each side (*l.h.c.* & *r.h.c.*). Size of cavities: left = .29 mm. × .14 mm.; right = .30 mm. × .16 mm. × 50 and reduced by  $\frac{1}{4}$ .

*a.c.a.* = arteria cerebri anterior. *FB.* = fore-brain. *hp.* = hypophysis.



flattened, its outer layer being much thickened and bulging into the cavity, and the wide opening in the optic stalk is connected with the fore-brain. The ectoderm opposite the vesicle is as yet only slightly thickened on the ventro-lateral side of the latter.

This embryo possesses a large premandibular head-cavity on each side of the fore-brain in the usual position medial and posterior to the optic vesicle (text-figs. 23 & 24, *l.h.c.* & *r.h.c.*). The dorsal portion of the cavity is somewhat irregular in shape with a small area marked off towards the median plane by a

Text-figure 24.



*Macropus ruficollis*. G.L. 67 mm.

Left head-cavity (*l.h.c.*) showing its lining of a single layer of epithelial cells.  
Size of cavity = .29 mm. × .14 mm. × 200.

constriction as in *Trichosurus*, embryo (*a*), 5 mm.; further ventrally, it assumes a more oval form (text-figs. 23 & 24, *l.h.c.* & *r.h.c.*), measuring on the left side .29 mm. × .29 mm. × .14 mm. and on the right .31 mm. × .30 mm. × .16 mm., the shortest measurement being the transverse one. It is lined throughout by a single layer of epithelial cells.

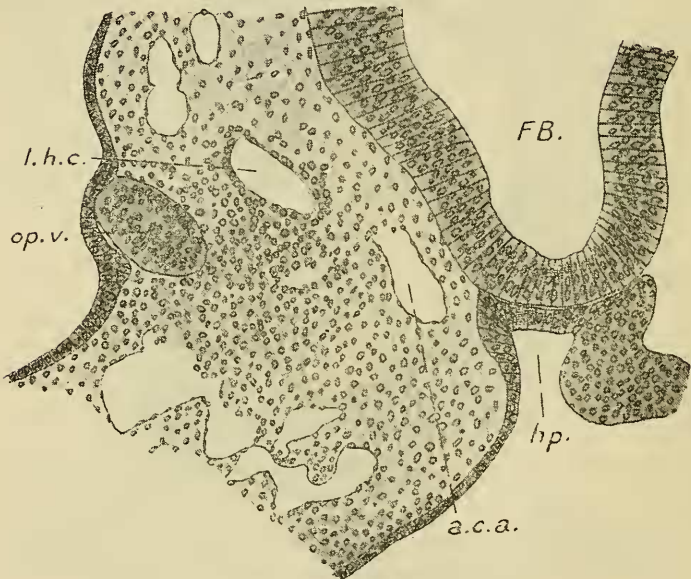
The abducens muscle complex, the intermediate mass and the primordium of the m. obliquus superior are united in the usual way, but their respective limits are difficult to determine

as their component cells are loosely connected and rather spread out, so that they are not easily distinguished from the surrounding mesenchyme. The primordium of the m. obliquus superior is more compact than the rest and forms a large rounded mass above the optic vesicle, posterior to and on the outer side of the supra-orbital branch of the trigeminal nerve.

PERAMELES spp. (Text-fig. 25.)

Our first stage of *Perameles* is an embryo of *P. nasuta* measuring 5.7 mm. at its greatest length. The primary optic vesicle is flattened and the outer layer thickened, and the optic stalk contains a wide cavity communicating with the fore-brain. The adjacent ectoderm is enlarged and slightly invaginated to form the primordium of the lens.

Text-figure 25.



*Perameles nasuta*. G.L. 5.7 mm.

Horizontal section through the head (S 4-1-11), showing the left head-cavity (*l.h.c.*) when at its largest.  $\times 110$ .

*a.c.a.* = arteria cerebri anterior. *FB.* = fore-brain. *hp.* = hypophysis.  
*op.v.* = optic cup.

A small very reduced head-cavity is to be seen on each side posterior and medial to the optic vesicle (text-fig. 25, *l.h.c.*). It is very irregular in form, is much broken up, and for the most part is bordered simply by mesenchyme cells, a definite

layer of epithelium having been observed only in the section figured where the cavity is larger than it is elsewhere. There appear to be proliferations of cells round parts of the cavity but no definite muscle-masses can be distinguished.

The *m. obliquus superior* and the *abducens* muscle-mass are connected by means of the intermediate mass and show the same relations as described for other genera. A portion of the intermediate mass is apparently joined with a side of the head-cavity but the limits between the parts are again difficult to make out.

In the next embryo, which measures 7 mm., the cavity of the optic vesicle is almost closed and the lens forms a hollow vesicle but the optic stalk is still widely open. Small head-cavities are again found, the one on the left side being larger and better developed than in the 5.7 mm. embryo, while that on the right is more or less broken up. On both sides a thickening is present on the postero-lateral side of the head-cavity and the primordium of the *m. obliquus inferior* extends down below the cavity; on the left a proliferating dorso-lateral bud is present.

In the 8.75 mm. embryo of *P. obesula* the cavities have almost disappeared and may be compared with the traces of the head-cavity still left in the 8.5 mm. embryo of *Trichosurus*. The muscles are developing as in the latter.

#### DIDELPHYS MARSUPIALIS. (Text-fig. 26.)

We had at our disposal only one embryo of *Didelphys* measuring 8.5 mm. The optic vesicle is completely invaginated and its cavity obliterated; the optic stalk on the right side contains a prominent cavity connecting it with the fore-brain but on the left it is almost solid, only a few very small hollow spaces remaining, and these are chiefly on the side next the brain. On the left side the lens has just separated off from the ectoderm but lies close to the latter and is of a remarkably small size, but on the right no lens could be seen and had apparently not yet begun to develop.

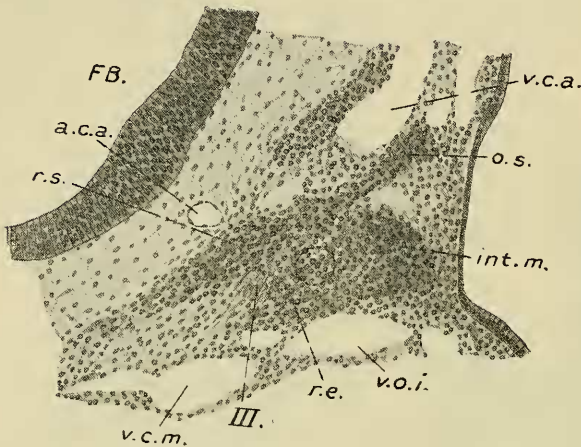
No head-cavities are present but in the usual position of the latter, posterior and dorsal to the eye, lies a condensed mass of mesenchyme cells from which the eye muscles are developing.

On careful examination, the postero-lateral side of this mass, which extends obliquely forwards in front of the *vena capitis medialis*, is recognised without difficulty as the *abducens* muscle-mass (text-fig. 26, *r.e.*); lying parallel to this, on the anterior side of the whole group of cells, we see the future *m. rectus superior* (text-fig. 26, *r.s.*), between the medial side of which and the *abducens* muscle-mass runs down the *oculomotor* nerve. The lateral side of the *abducens* muscle-mass is joined with the intermediate mass which, stretching forwards above the eye, is continued into an outgrowth corresponding to the primordium of the *m. obliquus superior* (text-fig. 26, *o.s.* and *int.m.*). The



intermediate mass is also united with the lateral side of the primordium of the m. rectus superior, thus recalling the connection of the intermediate mass with the postero-lateral wall of the head-cavity in other marsupials. The central region of the cell group is compact and as one passes further ventrally, below the section figured, the primordium of the m. obliquus inferior is seen to grow out downwards from this region, its approximate position being marked in the diagram by a broken circle (text-fig. 26). In still younger embryos it is possible that vestiges of a cavity may be present, but if so they become early obliterated.

Text-figure 26.

*Didelphys marsupialis*. G.L. 8.5 mm.

Horizontal section through the head (S2-4-11), showing the mass of mesenchyme dorsal to the optic cup, from which the eye muscles are developing. The broken circle indicates approximately the area from which, further ventrally, the primordium of m. rectus inferior grows out.  $\times 100$  and reduced by  $\frac{1}{4}$ .

*a.c.a.* = arteria cerebri anterior. *FB.* = fore-brain. *int.m.* = intermediate mass. *o.s.* = m. obliquus superior. *r.e.* = anterior portion of abducens muscle-mass. *r.s.* = m. rectus superior. *v.c.a.* = vena cerebri anterior. *v.c.m.* = vena capitis medialis. *v.o.i.* = vena orbitalis inferior. *III.* = oculomotor nerve.

The conditions in *Didelphys* are interesting, as they may possibly form a clue to the more accurate identification of the group of mesenchyme cells from which the eye muscles arise in higher mammals. Reuter ('97), as already mentioned, regards the eye muscles in the pig as originating from a single mass of mesenchyme cells. In the description of his earliest stage (G.L. 10 mm.) he says (p. 384):—"Sie [die allererste Anlage der Augenmuskeln] hat die Form einer gestielten Sichel und umgreift mit den beiden nach vorn gerichteten Schenkeln den Augensiel, während der dritte hintere Schenkel vom N. abducens fortgesetzt wird. Die Spitze des oberen Schenkels bildet

sich mit ihrem Nerven, dem N. trochlearis, am spätesten aus." By the second stage (G.L. 13 mm.):—"Die Muskulaturanlage wandert nach vorn gegen den N. opticus hin und verliert ihren hinteren Schenkel, welcher von der Vena jugularis nach vorn zusammengedrängt wird." It will be remembered that in *Trichosurus* (G.L. 7 mm.) the root of the vena cerebrialis anterior penetrates through the dorsal side of the larger anterior portion of the abducens muscle-mass; this does not occur in the specimen of *Didelphys* which has perhaps passed this stage in development.

#### DASYURUS VIVERRINUS.

A good series of embryos of *Dasyurus viverrinus* was examined and no signs of any head-cavities were observed. The small size of these embryos, however, makes it exceedingly difficult to identify any small vestiges of cavities which might possibly persist.

We may conclude from the preceding facts that the occurrence of well-developed premandibular head-cavities is characteristic of the Diprotodontia, large cavities being found in *Trichosurus*, *Phascolarctos*, *Phascalomys* and *Macropus*. In the Polyprotodontia, on the other hand, cavities may be present, as for example in *Perameles*, but only in the form of comparatively small irregular spaces, quite insignificant as compared with those in the former group, or they are altogether absent, as in *Dasyurus* and probably also in *Didelphys*, the muscles from the first somite then developing from a solid mesodermal mass as in higher mammals.

Although there are variations in the mode of proliferation from the walls of the premandibular cavity in the different genera, the later development of the eye muscles presents much similarity and *Trichosurus* may be regarded as typical.

#### CONCLUDING REMARKS.

From the foregoing observations we have further evidence of the unique position occupied by the marsupials in the Class Mammalia. The possession of well-developed premandibular head-cavities, as yet observed in no other mammals, recalls the conditions existing in many reptiles. These cavities correspond very closely with those found in the lizard (Corning, '99), in the snake (Oppel, '90) and in the Chelonia (Filatoff, '07 & Johnson, '13).

Owing to lack of material of early stages it has not been possible to determine the exact mode of origin of the cavities at the anterior end of the head in marsupials, or even to establish the existence of a median piece connecting the two across the middle line. The connecting piece in reptiles very often forms a wide cross-canal, which may persist until a comparatively late

stage or may disappear before the cavities have attained their maximum size. This variation is mentioned by Corning ('00) (p. 66):—"Aus den Oppel'schen Figuren, wie aus den meinigen, geht hervor, wie stark die Variationen sind, welche man in Bezug auf die Ausbildung des mittleren Verbindungsstückes zwischen den beiden Kopfhöhlen antrifft. Nicht selten bleibt die Verbindung noch in relativ später Zeit bestehen, in anderen Fällen ist sie schon zu einer Zeit verschwunden, wo die Höhlenbildung im lateralen Theile noch nicht auf ihrem Höhepunkt angelangt ist, in noch anderen sehen wir im Stiel einzelne kleinere Höhlenbildungen auftreten, die sich später mehr oder weniger vollständig zu einer grossen Höhle vereinigen."

In the 5 mm. embryo of *Trichosurus* and in the 6·7 mm. *Macropus*, the small median portion partially constricted off from the rest of the cavity (text-fig. 1, *n.*) may possibly coincide with the swollen part of the stalk, which runs from the somite to the middle line in *Argus fragilis* (called by Oppel the "Hals") and which takes a part in the formation of the head-cavity.

We have seen that the walls of the premandibular cavity, as in most other Vertebrates, give rise to the muscles innervated by the oculomotor nerve. In *Trichosurus* and probably also in *Phascalomys*, the primordium of the m. obliquus inferior and the common primordium of the mm. rectus inferior and rectus internus develop as solid outgrowths from the posterior and ventral walls, whilst the primordium of the m. rectus superior arises from the walls of a hollow evagination on the dorso-lateral side, the latter mode of origin resembling that of all the oculomotor muscles in *Lacerta* (Corning, '99). In *Phascolarctos*, elongated hollow outgrowths occur along the greater part of the posterior wall of the cavity, an extensive budding here taking place. The further development of these three muscles in the marsupials agrees very closely with that of the same muscles in *Chelydra* (Johnson, '13).

The m. rectus internus and the m. rectus inferior develop from a common primordium, the m. rectus internus first appearing as an offshoot from near the proximal end of the m. rectus inferior; this offshoot grows directly upwards and outwards to the anterior side of the bulbus. In *Chelydra*, according to Johnson ('13), the common primordium becomes transformed into "a solid elongate mass. By the 11 mm. stage a constriction has appeared, slightly beyond the middle of this mass, differentiating it into a proximal M. rectus inferior and a distal M. rectus medialis. .... The proximal end, which at first is continuous with the distal end of the M. rectus inferior, works up along the medial side of this muscle so that the final separation of the two takes place at their proximal ends, *i. e.* their ends of origin." No movement of this kind has been observed in *Trichosurus*, and if it occurs it must take place in the short interval between the 10 mm. and 11 mm. stages.

The abducens complex and the m. obliquus superior are difficult to identify in our earliest stages, but by comparison with slightly older embryos it is possible to make out their contours in the surrounding mesenchyme from which they are not easily distinguished. In our first stages, up to 8·5 mm., the primordia of both these muscles are united with the maxillo-mandibular mesenchyme by an intermediate mass of more loosely connected cells, the position of which is well seen in *Phascalomys* (text-fig. 21, p. 332). The m. obliquus superior arises from this intermediate mass as an upgrowth which extends forwards above the eye, the intermediate mass itself apparently degenerating. In the rabbit, Edgeworth ('03) regards the m. obliquus superior and the m. rectus externus as "specialised portions of the mandibular and hyoid myotomes which separate, the former late, the latter very early in development, from the upper ends of their respective myotomes" (p. 82). In *Chelydra*, according to Johnson ('13), the m. obliquus superior (p. 159) "grows forward as a stream of cells from the dorsal portion of the mesenchymal cell-mass which results from the second head somite," the ventral portion of the latter at the 5 mm. stage being in close contact with the mesoderm of the mandibular arch. If we compare these conditions with those in *Trichosurus*, *Phascalartos* and *Phascalomys*, we may conclude with some probability that the intermediate mass answers to the second somite of the head whose cavity is already obliterated, or in which a cavity has never developed, and from whose dorsal region the m. obliquus superior takes its origin. In *Chelydra* also, at a certain stage in development, the identification of the second somite is a matter of some difficulty. In the embryo of 7 mm. Johnson says (p. 142):—"The second head somite of the 7 mm. stage is of such indistinct and indefinite form that it may easily escape notice. It reaches here the most obscure phase of its development. The more or less conspicuous cavities of earlier stages have collapsed and broken down, and with their disappearance the cells of their walls are with difficulty distinguished from the intruding and intermingling mesenchymal elements."

No cavity is seen in the abducens muscle-mass, which in our earliest embryo is quite solid and shows a temporary attachment, as above mentioned, to the intermediate mass, this connection being probably a secondary phenomenon as in *Chelydra*, where it also occurs. It is possible that the intermediate mass, *i. e.* the second somite, may contribute towards the formation of the m. rectus externus as in some fishes (Dohrn, '04, Neal, '14), but we have no direct evidence of this in *Trichosurus*. The m. rectus externus and m. retractor bulbi develop exactly as in *Chelydra*; the origin of the m. retractor bulbi bearing no resemblance to that of the pig where, according to Renter ('97), p. 376:—"Dieser Muskel entsteht aus dem inneren Mantel des Augemuskelkelches durch Abspaltung von vorn nach hinten."

In *Chelydra*, however, the m. retractor bulbi separates off from the m. rectus externus at an early stage before the second somite has completely degenerated and when the m. rectus inferior and internus first begin to differentiate from each other, whereas in *Trichosurus* it only becomes an independent muscle at 17.5 mm. after the other muscles of the eye have assumed their final positions and at a time when the m. rectus inferior and internus are almost completely separated. The m. retractor bulbi in both animals is the last of the eye-muscles to reach its adult position.

The cranial nerves III, IV and VI arise from the brain and grow towards their respective muscles, their connection with the mesodermal somites being a secondary one as shown by Neal ('14). No independent origins in the muscles themselves are present as described by Filatoff ('07) in *Emys lutaria*. The oculomotor runs at its distal end into the proliferation on the postero-lateral wall of the head-cavity and breaks up into many fibres at the region where the m. obliquus inferior and m. rectus inferior first grow out, these two muscles being innervated at practically the same time; later, at the earliest indication of the m. rectus internus, fibres are seen to run into the root of the latter. The abducens develops in the typical manner and runs into the posterior end of the abducens muscle-mass; when the m. retractor bulbi grows forwards and separates off from the m. rectus externus, the nerve branches into the two muscles at the point where the former crosses the medial side of the latter. The trochlear, as is usually the case, arises later than the other two nerves. In *Trichosurus* it first appears at 8.5 mm. and does not reach the m. obliquus superior until 11 mm., when it penetrates into the posterior side of the medial end of this muscle.

#### Bibliography.

- '97. ALLIS, E. P., Jr.—“The Cranial Muscles and Cranial and First Spinal Nerves in *Amia calva*.” Journ. of Morph. vol. xii., 1897.
- '02. ——. “The Lateral Sensory Canals, the Eye Muscles, and the Peripheral Distribution of certain of the Cranial Nerves in *Mustelus levis*.” Quart. Journ. Micr. Sci. vol. xlv., 1902.
- '78. BALFOUR, F. M.—“A Monograph on the Development of Elasmobranch Fishes.” London, 1878.
- '04. BOEKE, J.—“Beiträge zur Entwicklungsgeschichte der Teleostier. II. Die Segmentierung des Kopfmesoderms, die Genese der Kopfhöhlen, das Mesectoderm der Ganglienleisten und die Entwicklung der Hypophyse bei den Muraenoiden.” Petrus Camper, 2 Deel. 1904.



- '99. BRAUS, H.—“Beiträge zur Entwicklung des Muskulatur und peripheren Nervensystems der Selachier.” *Morph. Jahrb.* Bd. xxvii., 1899.
- '99. CORNING, H. R.—“Ueber einige Entwicklungsvorgänge am Kopfe der Anuren.” *Morph. Jahrb.* Bd. xxvii., 1899.
- '00. ——. “Ueber die Entwicklung der Kopf- und Extremitätenmuskulatur bei Reptilien.” *Morph. Jahrb.* Bd. xxviii., 1900.
- '02. ——. “Ueber die vergleichende Anatomie der Augenmuskulatur.” *Morph. Jahrb.* Bd. xxix., 1902.
- '99. DAVIDOFF, M. VON.—“Ueber praeoralen Darm und die Entwicklung der Praemandibularhöhle bei den Reptilien.” *Festschrift f. C. von Kupffer*, 1899.
- '85. DOHRN, A.—“Studien zur Urgeschichte der Wirbelthierkörpers. VII. Die Entstehung und Differenzirung des Zungenbein- und Kiefer-Apparates des Selachier.” *Mitth. aus der Zool. Station zu Neapel.* Bd. vi., 1885.
- '90. ——. “XV. Neue Grundlagen zur Beurtheilung der Metamerie des Kopfes.” *Ibid.* Bd. ix., 1890.
- '91. ——. “XVI. Ueber die erste Anlage und Entwicklung der Augenmuskelnerven bei Selachiern und das Einwandern von Medullarzellen in die motorischen Nerven.” *Ibid.* Bd. x., 1891.
- '04. ——. “XXIII. Die Mandibularhöhle der Selachier.” “XXIV. Die Prämandibularhöhle.” *Ibid.* Bd. xvii., 1904 (a & b).
- '07. ——. “XXV. Der Trochlearis.” *Ibid.* Bd. xviii., 1907.
- '99. EDGEWORTH, F. H.—“On the Medullated Fibres of some of the Cranial Nerves and the Development of Certain Muscles of the Head.” *Journ. of Anat. & Phys.* vol. xxxiv., 1899.
- '03. ——. “The Development of the Head Muscles in *Scyllium canicula*.” *Journ. of Anat. & Phys.* vol. xxxvii., 1903.
- '07. ——. “The Development of the Head Muscles in *Gallus domesticus*, and the Morphology of the Head Muscles in the Sauropsida.” *Quart. Journ. Micr. Sci.* vol. li., 1907.
- '11. ——. “On the Morphology of the Cranial Muscles in some Vertebrates.” *Quart. Journ. Micr. Sci.* vol. lvi., 1911.
- '07. FILATOFF, D.—“Die Metamerie des Kopfes von *Emys lutaria*.” *Morph. Jahrb.* Bd. xxxvii., 1907.
- '91. FRORIEP, A.—“Referat über Entwicklungsgeschichte des Kopfes.” *Bonnet u. Merkel Ergebnisse*, Bd. i., 1891.
- '75. FÜRBRINGER, P.—“Untersuchungen zur vergleichenden Anatomie der Muskulatur des Kopfskelets der Cyclostomen.” *Jena Zeitschr. f. Naturw.* Bd. ix., 1875.
- '75. GOETTE, A.—“Die Entwicklungsgeschichte der Unke.” Leipzig, 1875.

- '88. GOETTE, A.—“Ueber die Entwicklung von *Petromyzon fluviatilis*.” Zool. Anz., xi Jahrg. No. 275, 1888.
- '01. GROSSER, O.—“Zur Anatomie und Entwicklungsgeschichte des Gefäßsystemes der Chiropteren.” I. anat. Instit. Wien, 1901.
- '95. — & BREZINA, E.—“Ueber die Entwicklung der Venen des Kopfes und Halses bei Reptilien.” Morph. Jahrb. Bd. xxiii., 1895.
- '90. HOFFMANN, C. K.—Reptilien. Bronn's Klassen und Ordnungen des Thier-reichs, Bd. vi., Abth. iii., 1890.
- '96. —. “Beiträge zur Entwicklungsgeschichte der Selachii.” Morph. Jahrb. Bd. xxiv. 1896. Fortsetzung: Morph. Jahrb. Bd. xxv. 1897, & Bd. xxvii. 1899.
- '13. JOHNSON, C. E.—“The Development of the Prootic Head Somites and Eye Muscles in *Chelydra serpentina*.” American Journ. of Anat. vol. xiv., 1913.
- '88. KASTSCHENKO, N.—“Zur Entwicklungsgeschichte des Selachierembryos.” Anat. Anz. Bd. iii., 1888.
- '01. LAMB, A. B.—“The Development of the Eye Muscles in *Acanthias*.” Amer. Journ. of Anat. vol. i., 1901.
- '09. MARCUS, H.—“Beiträge zur Kenntnis der Gymnophionen.” “III. Zur Entwicklungsgeschichte des Kopfes.” Morph. Jahrb. Bd. xl. Teil i., 1909.
- '10. —. “IV. Zur Entwicklungsgeschichte des Kopfes.” Teil ii., Festschr. f. R. Hertwig, Bd. ii., 1910.
- '81. MARSHALL, A. MILNES.—“On the Head Cavities and Associated Nerves of Elasmobranchs.” Quart. Journ. Micr. Sci. vol. xxi., 1881.
- '81. —, & SPENCER, BALDWIN.—“Observations on the Cranial Nerves of *Scyllium*.” Quart. Journ. Micr. Sci. vol. xxi., 1881.
- '87. MOTAIS.—“Anatomie de l'Appareil moteur de l'Œil de l'Homme et des Vertébrés.” Delahaye et Lecrosnier, Paris, 1887.
- '14. NEAL, H. V.—“The Morphology of the Eye Muscle Nerves.” Journ. of Morph. vol. xxv., 1914.
- '93. NUSSBAUM, M.—“Vergleichend-anatomische Beiträge zur Kenntnis der Augenmuskeln.” Anat. Anz. Bd. viii., 1893.
- '99. —. “Entwicklung der Augenmuskeln bei den Wirbeltieren.” Sitzber. der niederrhein. Ges. f. Natur- und Heilkunde. Bonn, 1899.
- '90. OPPEL, A.—“Ueber Vorderkopfsomiten und die Kopfhöhle von *Anguis fragilis*.” Arch. f. mikr. Anat. Bd. xxxvi., 1890.
- '87. ORR, H.—“Contribution to the Embryology of the Lizard.” Journ. of Morph. vol. i., 1887.
- '90. PLATT, JULIA B.—“The Anterior Head Cavities of *Acanthias*.” Zool. Anz. Bd. xiii., 1890.

- '91. PLATT, JULIA B.—“A Contribution to the Morphology of the Vertebrate Head, based on the study of *Acanthias vulgaris*.” Journ. of Morph. vol. v., 1891.
- '91. ——. “Further Contribution to the Morphology of the Vertebrate Head.” Anat. Anz. Bd. vi., 1891.
- '94. ——. “Ontogenetische Differenzirung des Ectoderms in *Necturus*.” Arch. f. mikr. Anat. Bd. xliii., 1894.
- '93. POLLARD, H. B.—“Observations on the Development of the Head in *Gobius capito*.” Quart. Journ. Micr. Sci. vol. xxxv., 1893.
- '97. REUTER, R.—“Ueber die Entwicklung der Augenmuskulatur beim Schwein.” Bonnet u. Merkel, Anat. Hefte, Bd. vii., 1897.
- '97. REX, H.—“Ueber das Mesoderm des Vorderkopfes der Ente.” Arch. f. mikr. Anat. Bd. l., 1897.
- '01. ——. “Ueber das Mesoderm des Vorderkopfes von *Larus ridibundus*.” Anat. Anz. Bd. xix., 1901.
- '05. ——. “Ueber das Mesoderm des Vorderkopfes der Lachmöwe.” Morph. Jahrb. Bd. xxxiii., 1905.
- '11. ——. “Neue Beiträge zur Entwicklung des Vorderkopfes der Vögel.” Morph. Jahrb. Bd. xliii., 1911.
- '02. SALVI, G.—“L'origine et il significato delle fossette laterali dell' ipofisi e delle cavità premandibolari negli embrioni di alcuni Sauri.” Archiv. Ital. di Anat. et di Embriol. vol. i., 1902.
- '79. SCOTT, W. B., & OSBORN, H. F.—“On some Points in the early Development of the Common Newt.” Quart. Journ. Micr. Sci. vol. xix., 1879.
- '93. SEWERTZOFF, A. N.—“Studien zur Entwicklungsgeschichte des Wirbeltierkopfes. I. Die Metamerie des Kopfes des elektrischen Rochens.” Bull. de la Soc. Imp. d. Natur. de Moscou. 1898.
- '96. TIESING, B.—“Ein Beitrag zur Kenntnis der Kiefer- und Kiemenmuskulatur der Haie und Rochen.” Jena Zeitschr. f. Naturw. Bd. xxx., 1896.
- '77. WEBER, M.—“Ueber die Nebenorgane des Auges der Reptilien.” Arch. f. Naturg. Bd. xliii., 1877.
- '86. ——. “Studien über Säugethiere. Ein Beitrag zur Frage nach dem Ursprung der Cetaceen.” 1886.
- '83. VAN WILHE, J. W.—“Ueber die Mesodermsegmente und die Entwicklung der Nerven des Selachierkopfes.” Naturk. verh. der koninkl. Akademie, Deel xxii., 1883.
- '86. ——. “Ueber Somiten und Nerven im Kopfe von Vögel- und Reptilienembryonen.” Zool. Anz. Bd. ix., 1886.
- '08. ZIEGLER, H. E.—“Die phylogenetische Entstehung des Kopfes der Wirbelthiere.” Jena Zeitschr. f. Naturw. Bd. xliii., 1908.
- '98. ZIMMERMANN, K. W.—“Ueber Kopfhöhlenrudimente beim Menschen.” Arch. f. mikr. Anat. Bd. liii., 1898.

## EXPLANATION OF THE PLATES.

## Lettering.

<i>aln.</i> = ali-nasal cartilage.	<i>r.b.</i> = m. retractor bulbi.
<i>cil.g.</i> = ciliary ganglion.	<i>r.e.</i> = m. rectus externus.
<i>FB.</i> = fore-brain.	<i>r.i.</i> = m. rectus internus.
<i>e.</i> = eyeball.	<i>r.inf.</i> = m. rectus inferior.
<i>l.</i> = lens.	<i>r.s.</i> = m. rectus superior.
<i>n.c.V.</i> = naso-ciliary branch of the trigeminal nerve.	III. = oculomotor nerve.
<i>o.inf.</i> = m. obliquus inferior.	IV. = trochlear nerve.
<i>op.c.</i> = optic cup.	V. = trigeminal nerve.
<i>op.s.</i> = optic stalk.	VI. = abducens nerve.
<i>o.s.</i> = m. obliquus superior.	+ = band of mesodermal cells.

## PLATE I.

*Trichosurus vulpecula.* G.L. 9.5 mm. (V. '01).

Fig. 1. Coloured drawing of wax-plate model, posterior view, showing the anterior (*r.e.*), and the posterior (*r.b.*) portions of the abducens muscle-mass, the primordium of the m. obliquus inferior (*o.inf.*) extending down from the postero-lateral corner of the solid mass of mesoderm representing the former head-cavity. The primordium of the m. rectus superior (*r.s.*) stretches up above the optic cup from the dorso-lateral side of the same mass. Nerve III. (III.) runs down just in front of the abducens muscle complex and into the hinder end of the latter runs Nerve VI. (VI.) A band of mesodermal cells (+) is seen to extend out towards the ventral border of the eyelid.  $\times 300$  and reduced by  $\frac{1}{3}$ .

2. Anterior view, showing the primordium of the m. obliquus superior (*o.s.*) with its narrow prolongation lying anteriorly to the optic cup (*op.c.*), the primordium of the m. rectus inferior (*r.inf.*), extending forwards below the optic stalk from the medial side of the m. obliquus inferior (*o.inf.*). The primordium of the m. rectus superior (*r.s.*) is again seen. The naso-ciliary branch (V.) of Nerve V. runs forwards below the m. obliquus superior. *l*=lens. The band of mesodermal cells (+) extending out to the ventral border of the eyelid is again seen.  $\times 300$  and reduced by  $\frac{1}{3}$ .

## PLATE II.

*Trichosurus vulpecula.* G.L. 15 mm.

Fig. 3. Coloured drawing of wax-plate model, anterior view, showing the m. obliquus superior (*o.s.*), the m. obliquus inferior (*o.inf.*), and the m. rectus inferior (*r.inf.*) from which branches out the m. rectus internus (*r.i.*). Nerve IV. (IV.) runs into the postero-medial side of the m. obliquus superior (*o.s.*).  $\times 150$  and reduced by approximately  $\frac{2}{3}$ .

4. Posterior view, showing the m. rectus superior (*r.s.*), the m. retractor bulbi (*r.b.*) still connected with the m. rectus externus (*r.e.*), and the m. obliquus inferior (*o.inf.*) in which runs Nerve III. Nerve VI. is seen at the point of union of the m. rectus externus and the m. retractor bulbi. A faint dotted line indicates approximately the line of junction between the m. rectus externus and the m. retractor bulbi.  $\times 150$  and reduced by approximately  $\frac{2}{3}$ .
5. Ventral view, showing the distal end of the m. retractor bulbi (*r.b.*) which is growing forwards round the optic stalk, the m. obliquus inferior (*o.inf.*) attached to the ali-nasal cartilage (*aln.*), and the ciliary ganglion (*cil.g.*) lying below the optic stalk. Nerve III. is seen to run out from the m. rectus inferior (*r.inf.*) into the m. obliquus inferior.  $\times 150$  and reduced by approximately  $\frac{2}{3}$ .